

The influence of vegetation structure and composition on invasibility by *Pinus radiata* in the Blue Mountains, NSW

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Abstract: The exotic tree species *Pinus radiata* D. Don (in the family Pinaceae) has successfully spread from commercial plantations into adjacent vegetation in southeastern Australia. Identifying factors facilitating spread will aid the control of current invasions and the prediction of future invasion events. The structure and composition of vegetation can have an important role in determining community resilience to invasion. Two dry eucalypt sclerophyll woodlands in the Blue Mountains west of Sydney known to be invaded by *Pinus radiata* were surveyed to investigate the influence of eucalypt presence, species diversity, species composition and vegetation cover on the extent and density of invasion. Relationships between community characteristics and the level of pine invasion were weak and variable. Pines were found growing in plots with 0–70% understorey cover and 5–90% ground cover, and in areas of both high and low eucalypt diversity and presence, illustrating the high invasion potential of *Pinus radiata*.

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Introduction

The impact of invading organisms on the biodiversity of ecosystems worldwide has been well documented (Hobbs & Mooney 1986, Vitousek et al. 1987, Mooney & Drake 1989, Mack & D'Antonio 1998, Groves & Willis 1999, Pimental et al. 2000). Much of the attention of invasion biologists has focussed on identifying attributes of invaders (Noble 1989, Mack 1992, Rejmanek & Richardson 1996) and invaded communities (Crawley 1987, Levine & D'Antonio 1999, Symstad 2000) in the hope of better understanding invasion mechanisms and aiding the mitigation of current invasions and prediction of future invasion events. However, efforts to identify a suite of characteristics common to invading organisms and vulnerable communities have largely been unsuccessful. In the absence of accurate generalisations regarding community invasibility, detailed site- and species-specific investigations continue to be useful approaches.

The exotic tree species *Pinus radiata* D. Don (in the family Pinaceae) has successfully invaded areas of native vegetation in southeastern Australia including Victoria (Minko & Aeberli 1986, cited in Richardson et al., 1994), New South Wales (Williams & Wardle 2005), Australian Capital Territory (Burdon & Chilvers 1977, Lindenmayer & McCarthy 2001) and South Australia (Virtue & Melland 2003). The spread of seed from large commercial plantations of the species into adjacent natural areas has led to the establishment of self sown individuals (wildlings) that are capable of dominating the landscape and negatively impacting the local ecosystem. Pine trees form dense stands and have the ability

to significantly affect the structure and function of the native environment (Versfield & Van Wilgen 1986, Richardson et al. 1994a, Richardson et al. 1994b).

Factors governing the success of an invader include the number of propagules entering the environment (referred to as propagule pressure), characteristics of the new species and the susceptibility through time of the new environment to invasion (Lonsdale 1999). Plantations of *Pinus radiata* represent a large constant seed source and it is assumed that the number of propagules entering adjacent areas is high, and that seed availability is a non-limiting factor (Wardle et al., unpublished data). Key plant characteristics recognised as facilitating pine invasions include 1) the short juvenile period and short interval between large seed crops that results in early and regular production of seed and hence rapid population growth (Rejmanek & Richardson 1996); 2) the small mass and high wing loading of many pine seeds that can increase their dispersal capabilities (Van Wilgen & Siegfried 1986) and their potential for spread. Given this capacity of pines to invade, and the large seed source that plantations provide, it is likely that characteristics of the recipient habitat are having a large influence on invasion success.

A number of components of vegetation communities have been implicated in either facilitating or preventing the influx of invaders. One of the key and yet most controversial ideas relating to invasion theory is that areas of high species diversity are less prone to invasion (Elton 1958, Fox & Fox 1986). Communities with high species richness should

in theory deplete limiting resources more effectively and thus prevent invaders from competing for those resources (MacArthur & Wilson 1967). However, this theory remains highly contentious and has more recently been challenged by the idea that the nature of the relationship between native and exotic species is highly scale dependent (Fridley et al. 2004, Herben et al. 2004). It is possible that the negative relationship between exotic and native species richness commonly observed in small scale experimental studies is an artefact of sample size and does not reflect any real negative interaction between the two. At larger scales plots will display greater variation in species richness and are likely to include more species of both native and invasive species resulting in a positive relationship between native and exotic species richness (Fridley et al. 2004).

Few studies have investigated the relationship between *Pinus radiata* invasion and species diversity. However, contrary to the theory that high native species diversity provides resistance to invasion by exotics, Lindenmayer and McCarthy (2001) found an increase in pine occurrence with increasing native tree species diversity within eucalypt forest remnants in southern New South Wales. South African fynbos, a shrubland vegetation very rich in species diversity is particularly susceptible to invasion by *Pinus* species (Richardson & Brown 1986). A greater understanding of the specific mechanisms of interaction between pines and indigenous vegetation at small scales may shed light on the ability of native species diversity to provide resistance to invasion.

Pinus radiata plantations in Australia are established across a broad range of climates and soil types with a variety of vegetation types that appear to differ in their susceptibility to invasion. Evidence from pine invasions in Australia suggests that forest types that vary in their canopy species will display differing levels of resistance to invasion. Lindenmayer and McCarthy (2001) reported significant differences in the probability of occurrence of *Pinus radiata* wildlings between forest types dominated by *Eucalyptus dives* and *Eucalyptus bridgesiana* which were more likely to be invaded, than areas dominated by other *Eucalyptus* species including *Eucalyptus viminalis* and *Eucalyptus pauciflora*. Other Eucalypt forests, such as those dominated by *Eucalyptus blakelyi* have been found to be relatively resistant to invasion (Minko & Aeberli 1986 cited in Richardson et al., 1994).

A recent study by Williams and Wardle (2005) found two dry eucalypt woodlands in the Blue Mountains, west of Sydney to be equally invadable by *Pinus radiata*. The authors recorded high pine densities of up to 1000 individuals per hectare and isolated pines growing at distances of up to 4 km from the plantation. Pine occurrence was highly variable with large scale aggregation of individuals (Williams and Wardle, 2005). Detailed investigations of specific structural and compositional components of vegetation at the study sites may provide insight into factors facilitating invasion. This study quantified eucalypt basal area, species diversity, species composition

and vegetation cover within areas invaded by *Pinus radiata* to determine their influence on the extent and density of invasion.

Methods

Study sites

The study took place in two state forests situated in the upper Blue Mountains in the Central Tablelands of New South Wales. Newnes State Forest (150°12'E, 33°24'S; altitude 1000–1170 m) is located approximately 7.5 km north-east of Lithgow, NSW and encompasses a 51 year old, 2000 hectares *Pinus radiata* plantation. Lidsdale State Forest (150°3'E, 33°26'S; altitude 900–1000 m) is situated approximately 7 km north-west of Lithgow and includes a 46 year old, 580 hectares *Pinus radiata* plantation.

Average maximum temperatures in January, the hottest month are 23.2°C for Newnes State Forest and 24.6°C for Lidsdale State Forest. Average minimum temperatures for July, the coldest month, are -0.8°C at Newnes and -0.3°C at Lidsdale. Average annual rainfall is higher at Newnes (1072 mm) than at Lidsdale (870 mm). Seasonality is consistent at both sites with the majority of rain falling between January and March; July and August are the driest months (Bureau of Meteorology).

The two State Forests differ in their vegetation composition and soil type. The Newnes vegetation occurs on Sydney Basin Triassic sediments. Soils are characterised by earthy sands and shallow lithosols/siliceous sands (King 1993). Lidsdale is characterised by shallow stony lithosols and yellow podzolic soils derived from Devonian Lambie Group quartzites, sandstones, siltstones and claystones (King 1993).

The study area at Newnes State Forest has been described by Benson and Keith (1990) as 'Newnes Plateau Woodland' and is dominated by *Eucalyptus oreades* and *Eucalyptus sieberi*. The northern edge of the plantation is 'Blue Mountains Sandstone Plateau Forest' and is dominated by *Eucalyptus sieberi* and *Eucalyptus piperita*. This area was subject to a moderate intensity fire in December 2002. The understorey is an open shrub layer dominated by *Acacia terminalis*, *Hakea dactyloides*, *Banksia marginata* and a variety of *Leptospermum* species. The smaller shrub layer consists of *Boronia microphylla*, *Hibbertia obtusifolia*, *Lomatia silaifolia* and *Monotoca scoparia*. Common ground species were *Lomandra multiflora*, *Lomandra glauca* and the grass *Chionochloa pallida*. The vegetation at Lidsdale belongs to the "Mount Walker Complex" (Benson & Keith 1990). Vegetation structure is mainly woodland and dominated by *Eucalyptus mannifera*, *Eucalyptus dives* and *Eucalyptus bridgesiana*. The understorey is an open shrub layer with *Acacia dealbata*, *Leptospermum juniperinum* and *Leptospermum polyanthum*. Common ground species include *Lomandra longifolia* and *Lomandra multiflora* and the grass *Chionochloa pallida*.

Field Survey

The field survey was conducted between February and August 2003. At each site, pine occurrence was recorded within 20 m by 20 m plots located along six transects placed perpendicular to the plantation boundary (excluding transect 1 at Lidsdale which unavoidably ran parallel to a second plantation boundary when placed perpendicular to the first). Transects were placed on multiple borders of the plantation and ended when pines were no longer present or difficult terrain prevented further investigation. Transects ranged in length from 150 m to 2200 m at Newnes and from 200 m to 750 m at Lidsdale. Plots were placed in the nearest vegetation to the plantation edge, avoiding any forestry roads or fire breaks. The distance between plots varied from 100 m to 200 m to reflect changes in pine density. The height and diameter at breast height (dbh: 1.4 m) of *Pinus radiata* and eucalypt individuals were recorded for 28 plots at Newnes and 23 plots at Lidsdale. Plots were labeled with the letter 'N' or 'L' denoting Newnes or Lidsdale, followed by the transect number and a letter indicating the position of the plot within the transect. The dbh and height of tree species other than *Pinus radiata* were recorded for those with a dbh greater than 10 cm. The identification and percentage cover of dominant ground and understorey species were recorded for each plot.

The presence of forestry roads surrounding the plantation meant that the distance between the edge of a plantation and the location of the first plot in native vegetation typically ranged from 30 m to 70 m. However, for ease of analysis these plots are referred to as 'adjacent' plots located 50 m from the plantation. Plots greater than 50 m from the plantation are referred to as 'far' plots. Pine abundance is greatest within adjacent plots at both sites (Williams & Wardle 2005) indicating that propagule pressure is highest close to the plantation. At distances away from the plantation, where propagule pressure is reduced, it is more likely that factors such as vegetation are driving pine distribution.

Data analysis

To examine the relationship between species diversity and the level of invasion, correlations between Simpson's diversity index (S) and the number of species and pine abundance per plot were calculated using Pearson's correlation coefficient. Correlations were calculated for all plots combined, far plots, adjacent plots and plots combined on the basis of direction from the plantation.

Species composition data was analysed using PRIMER v5.2 (Plymouth Marine Laboratories 2001). Percentage cover estimates for each species within a plot were the basis of this analysis. Similarities in composition between samples (plots) were determined using non-metric multidimensional scaling (NMDS) using the Bray-Curtis similarity coefficient

(Bray & Curtis 1957). The process is non-metric because samples are ranked in terms of their similarities. NMDS ordinations position samples on the basis of these ranks in multidimensional space. The closer samples are to each other, the more similar they are. To examine the relationship between species composition and the level of pine invasion, plots were categorised on the basis of pine occurrence. Pine abundance classes were, Low: < 20 pines, Medium: 21–40 pines, High: 41–60 pines and Very High: > 60 pines. Basal area categories were, Low: < 1m²/ha, Medium: 1–5 m²/ha, High: > 5–10 m²/ha and Very High: > 10m²/ha. If species composition is driving pine distribution the expectation is to see plots with similar species assemblages experiencing similar levels of pine invasion. On an NMDS plot this translates to a clustering of samples based on their pine abundance or basal area categories.

To establish if samples within pine categories were significantly different in their species composition, one-way ANOSIMs (PRIMER) were calculated. ANOSIM is analogous to ANOVA as it compares between-group and within-group variation using similarity ranks (Quinn & Keough 2002). An R statistic is calculated to test the null hypothesis that there is no difference between categories. R values greater than 0.75 indicate good separation of groups, R values greater than 0.5 suggest overlapping but clearly different groups, and values lower than 0.25 are barely separable (Clarke & Gorley 2001). Significance is determined by randomly reallocating samples within classes and calculating sample R values. The percentage of times that R is greater than the sampled R indicates whether the samples are significantly different (Clarke 1993). For any categories that were deemed significantly different from each other, SIMPER (PRIMER) analysis was performed. SIMPER (similarity percentages) identifies the species that are contributing most to the average dissimilarity between two groups (Clarke & Gorley 2001). To investigate patterns further, plots placed adjacent to the plantation were omitted from ordinations and the analysis repeated.

To examine the influence of vegetation cover on susceptibility to invasion, the relationship between total pine abundance, pine seedling abundance and percentage vegetation cover was determined using Pearson's correlation coefficient, for all plots, adjacent and far plots. It is important to realise that vegetation structure and density change with time and that present levels of cover may not represent the environment during the initial establishment of pines. Investigations of seedling abundance may provide more insight into the relationship between vegetation cover and the level of invasion as the number of seedlings in a plot will reflect the current susceptibility of the vegetation to invasion. The relationship between eucalypt basal area and pine basal area was calculated using Pearson's correlation coefficient. Eucalypt diversity within plots was also examined to determine their influence on pine occurrence.

Results

Species diversity

The relationship between Simpson's Diversity Index and pine occurrence was not significant at Newnes ($p > 0.01$) and significantly negative ($p < 0.01$) at Lidsdale (Fig. 1). Negative correlations between pine abundance and species diversity were frequent (Table 1). At Newnes, significantly ($p < 0.01$) negative relationships were found between pine abundance and the number of species in all except the south-west and pooled far plots. Significant ($p < 0.05$) correlations were found between the Simpson diversity index and pine abundance in all but the southern plots and the far plots combined at Lidsdale.

Despite these significant results, the relationship between species diversity and the level of invasion was far from conclusive. Plots with high numbers of species experienced varying levels of pine invasion. At Newnes, two plots located at an equal distance and direction from the plantation contained the same number of species and experienced a more than two fold difference in pine abundance, containing 24 and 55 pine individuals respectively. This pattern was also observed at Lidsdale. Three plots located adjacent to the plantation boundary each had 16 species present, yet they contained 50, 24 and 16 pine individuals respectively.

Species composition

All species

NMDS ordinations of plant species composition at Newnes and Lidsdale revealed no indication of association of assemblages within pine abundance categories (Figs 2 and 3). ANOSIM showed that there was no significant difference among pine abundance classes for either Newnes ($R = 0.07$, $p = 0.251$) or Lidsdale ($R = 0.172$, $p = 0.051$). Categorisation of plots on the basis of basal area yielded similar results (Newnes $R = 0.127$, $p = 0.15$; Lidsdale $R = 0.011$, $p = 0.44$). Exclusion of plots adjacent to the plantation revealed a significant ($p < 0.05$) difference between pine basal area categories at Newnes (Fig. 4). SIMPER analysis showed that *Eucalyptus pauciflora* (25.78%) and *Eucalyptus piperita* (10.78%) were contributing most to the difference between medium and low basal area categories. Plots of medium pine basal area were characterised by high *Eucalyptus pauciflora* and low *Eucalyptus piperita* abundance. SIMPER also indicated that a greater abundance of *Eucalyptus piperita* in plots of low pine basal area was contributing most (14.5%) to the difference between high and low basal area categories.

Canopy species

NMDS ordinations of eucalypt species composition at Newnes and Lidsdale (Figs 5 and 6) showed no significant

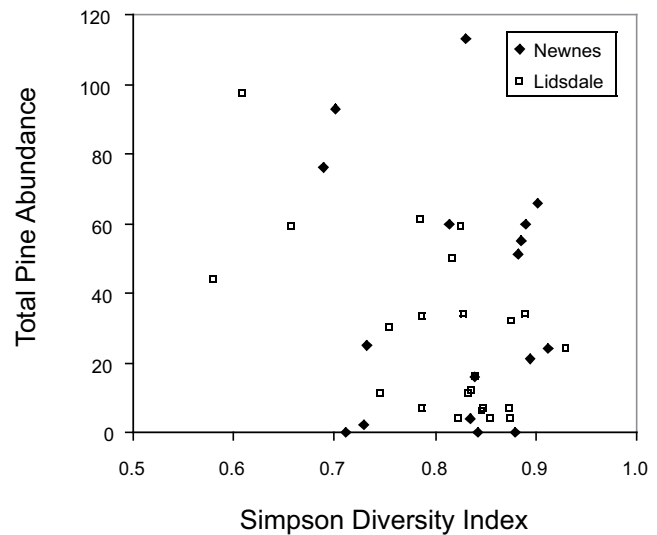


Fig. 1. Species diversity versus pine abundance for 17 plots at Newnes ($r = -0.076$) and 23 plots at Lidsdale ($r = -0.59$). This relationship was significant ($p < 0.01$) at Lidsdale.



Fig. 2. NMDS ordination of plant species composition (excluding pines) at Newnes (Stress = 0.15). Pine abundance classes L: < 20 pines, M: 21-40 pines, H: 41-60 pines, VH: > 60 pines

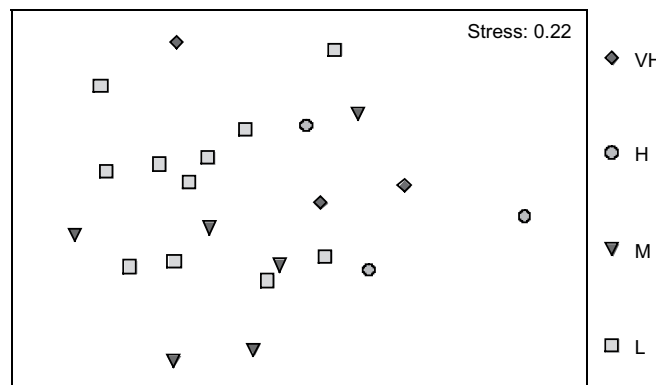


Fig. 3. NMDS ordination of plant species composition (excluding pines) at Lidsdale (Stress = 0.22). Samples are divided into pine abundance classes L: < 20 pines, M: 21-40 pines, H: 41-60 pines, VH: > 60 pines.

Table 1. Pearson's correlation coefficients for *P. radiata* abundance and the number of species and the Simpson diversity index.* Significant at $p = 0.05$, ** Significant at $p = 0.01$

	Plots (Sample size)	Number of species	Simpson diversity index
NEWNES	All (17)	-0.51*	-0.07
	Adjacent (8)	-0.65*	-0.27
	Far (9)	0.32	-0.08
	South-east (13) (Transects 1 and 2)	-0.55*	-0.17
	South-west (4) (Transects 3 and 4)	0.74	0.63
LIDSDALE	All (23)	-0.39*	-0.59*
	Adjacent (7)	-0.31	-0.85**
	Far (16)	-0.38	-0.34
	Eastern (5) (Transect 3 and 6)	-0.07	-0.97**
	Southern (8) (Transects 4 and 5)	-0.29	0.06

difference within pine abundance or basal area classes on the basis of eucalypt presence. Exclusion of plots adjacent to the plantation boundary did not reveal a significant influence of eucalypt composition.

When plots were pooled for each site, the overall relationship between pine and eucalypt abundance and basal area was negative at both sites (Table 2), suggesting competition between the two species. This result was only significant ($p < 0.01$) at Lidsdale. A consideration of this relationship within transects produced varying results. At Newnes, the relationship between eucalypt abundance and *Pinus radiata* abundance varied from a significantly ($p < 0.05$) negative interaction in transects 2 and 6 to no association in transect 1. At Lidsdale, correlations were highly negative with significant results observed for 3 of the 5 transects investigated. However, non-significant positive associations were also found for pine and eucalypt abundance within transect 1 and basal area in transect 4.

Mean eucalypt abundance in plots adjacent to the plantation was less than in far plots (Fig. 7). This result was significant for both Newnes ($F_{1,22} = 4.63$; $p = 0.043$) and Lidsdale ($F_{1,21} = 7.25$; $p = 0.014$). Mean eucalypt abundance in far plots was significantly greater at Newnes compared with far plots at Lidsdale ($F_{1,29} = 9.43$; $p = 0.005$). The mean eucalypt basal area in far plots at Lidsdale was 22.1 m²/ha, a value that is comparable with earlier studies of the area (Knights 1983), but significantly less than that recorded for Newnes (Basal area = 30.9 m²/ha; $F_{1,29} = 5.43$; $p < 0.027$).



Fig. 4. NMDS ordination of species composition (excluding pines) within far plots at Newnes. Pine basal area classes Low: less than 1 m²/ha, Medium: 1–5 m²/ha, High: 5–10 m²/ha (Stress = 0.05). ANOSIM showed significant differences between high and low ($R = 0.509$, $p = 0.048$) and between Medium and Low ($R = 0.964$, $p = 0.048$) basal area categories.



Fig. 5. NMDS ordination of Eucalypt species composition at Newnes (Stress = 0.14). L: < 20 *P. radiata* individuals, M: 20–40, H: 40–60, VH: > 60. ANOSIM revealed no significant separation of pine abundance ($R = 0.172$, $p = 0.09$) or basal area ($R = 0.164$, $p = 0.1$) classes.



Fig. 6. NMDS ordination of Eucalypt species composition at Lidsdale (Stress = 0.17). L: < 20 *P. radiata* individuals, M: 20–40, H: 41–60, VH: > 60. ANOSIM revealed no significant separation of pine abundance ($R = 0.135$, $p = 0.12$) or basal area ($R = 0.037$, $p = 0.39$) classes.

The general negative relationship between pine and eucalypt abundance is illustrated in Figures 8B and 9B. Two of the most noticeable exceptions to this trend include plot 1F at Newnes and plot 5D at Lidsdale. Plot N1F was dominated by *Eucalyptus pauciflora* and had the highest eucalypt basal area of all plots (67m²/ha). Despite this large eucalypt presence, 76 pines were found growing here. Similarly, plot L5B, dominated by high numbers of *Eucalyptus mannifera* and *Eucalyptus dives* had 34 pines growing. Both of these plots were characterised by large numbers of pine seedlings and a few highly reproductive trees retaining large numbers of cones (620 cones and 60 seedlings in N1F; 131 cones and 22 seedlings in L5B; Wardle et al. unpublished data).

Eucalyptus composition varied notably across both study sites. Some plots were dominated by one species, while others contained up to 4 different species. *Eucalyptus oreades* dominated canopy composition at Newnes and was found throughout the study site appearing to have no influence on pine occurrence (Fig. 8). The next most common species, *Eucalyptus piperita*, found in association with *Eucalyptus oreades*, was restricted to plots with less than 9m²/ha of pine (Fig. 8). Plots with greater than 9m²/ha of pine and free of *Eucalyptus piperita* were all located in Transect 1. *Eucalyptus mannifera* was the most common species at Lidsdale occurring in plots with varying levels of pine abundance and basal area (Fig. 9). *Eucalyptus dives* and *Eucalyptus bridgesiana* were locally dominant in some areas. There appeared to be little influence of *Eucalyptus* composition on the pattern of pine occurrence at Lidsdale.

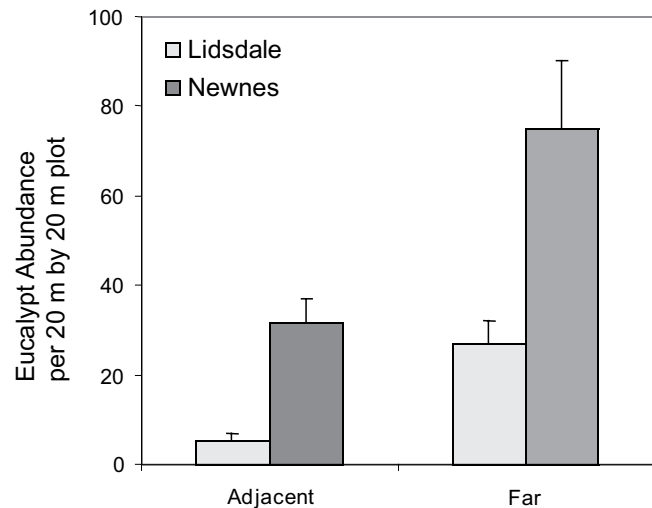


Fig. 7. Average (+SE) Eucalypt abundance in far and adjacent plots at both sites.

Vegetation structure

Levels of vegetation cover in the study plots ranged considerably, from 0 %–70 % understorey cover and from 5 %–90 % groundcover. Weak and varying relationships between vegetation cover and pine presence were found (Table 3). A significant ($p = 0.018$) positive correlation was found between canopy cover and pine seedlings in the adjacent plots at Lidsdale. However, this relationship was driven by the results of one plot which displayed the highest level of canopy cover (15%) and contained the highest number of seedlings (77).

Table 2. Relationship between eucalypt and pine occurrence. Number of plots (n) and Pearson's correlation coefficients for *P. radiata* and eucalypt basal area and abundance. Transects with two or less plots containing eucalypt and *P. radiata* data were omitted.

* Significant at $p = 0.05$, ** Significant at $p = 0.01$.

	NEWNES Correlation coefficients			LIDSDALE Correlation coefficients		
	n	Abundance	Basal Area (m ² /ha)	n	Abundance	Basal Area (m ² /ha)
All plots	24	-0.212	-0.215	23	-0.426*	-0.436*
Adjacent plots	9	-0.487	-0.420	7	0.431	-0.675
Far plots	15	0.081	-0.176	16	-0.337	0.183
Transect 1	7	-0.003	-0.430	6	0.653	-0.796*
Transect 2	6	-0.797*	-0.296	4	-0.996**	-0.278
Transect 3				3	-0.995*	-0.54
Transect 4				4	-0.734	0.729
Transect 5				4	-0.697	-0.871
Transect 6	6	-0.81*	-0.480			

Correlations between understorey cover and pine occurrence were inconsistent between sites. This relationship was negative across plots at Lidsdale and was strongest for total pines in the far plots ($r = -0.47, p = 0.065$). There was little influence of understorey cover on pine distribution at Newnes.

In general, only weak correlations between groundcover and pine occurrence were witnessed. A significant ($p < 0.05$) negative relationship between pine seedlings and groundcover was found in adjacent plots at Newnes. A significant ($p < 0.05$) positive relationship was found between total pine abundance and groundcover in far plots at Newnes.

Discussion

Significant negative relationships between species diversity and pine abundance were witnessed at both sites, providing some evidence for the hypothesis that species rich communities are resistant to invasion (Elton 1958, Fox & Fox 1986). However, the small sample size of plots considered and the varying level of pine abundance in plots with similar species composition suggest that this result must be interpreted with caution.

Furthermore, plots located adjacent to the plantation were often characterised by low species diversity and high pine abundance resulting in strong negative relationships between the two. In contrast, this relationship was weak and non-significant in far plots. These results may reflect higher levels of disturbance in areas close to the plantation. Lower *Eucalyptus* abundance witnessed in adjacent plots and the presence of cut stumps suggests that selective logging has occurred within these areas. Forestry activities including vegetation removal and hazard reduction burning lead to increased light levels and reduced vegetation cover, which are known to facilitate pine establishment (Richardson et

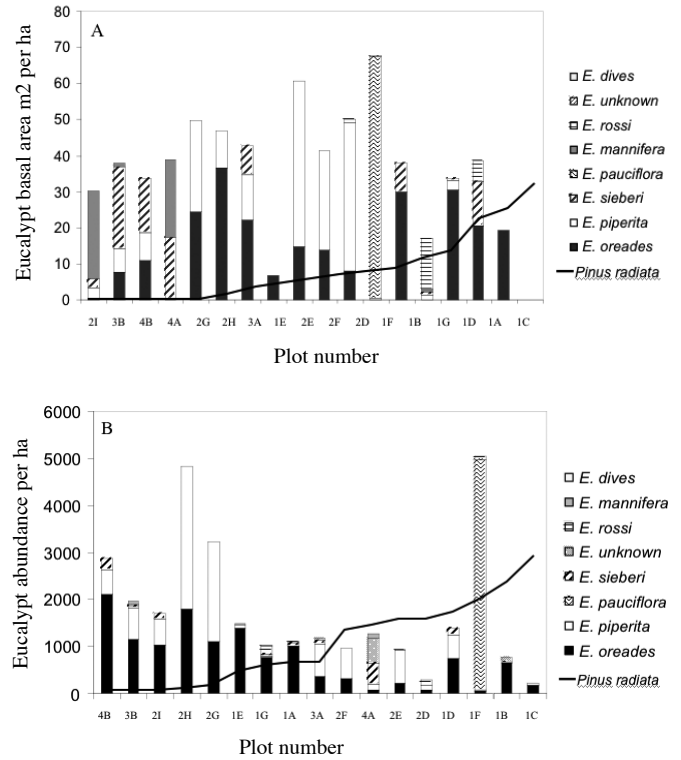


Fig. 8. Eucalypt composition versus increasing pine occurrence at Newnes. A. Basal Area m² per

al. 1994b). Observations of *Pinus radiata* invasion in Chile have also indicated that the level of disturbance on the forest edge is an important determining factor of invasion success (Bustamante et al. 2003). An area subjected to recent fire and logging was found to be severely invaded while pine spread was limited to the forest edge of a fragment experiencing comparatively low levels of disturbance.

Table 3. Correlation coefficients for vegetation cover percentages and pine presence at Newnes and Lidsdale. Far plots are those located greater than 50m from the plantation boundary.

* Significant at $p < 0.05$

PLOTS		NEWNES			LIDSDALE		
		All	Adjacent	Far	All	Adjacent	Far
Canopy Cover	Total pines	-0.39	-0.21	-0.35	-0.04	0.49	-0.37
	Pine seedlings	-0.46	-0.36	-0.43	0.27	0.83*	-0.34
Understorey Cover	Total pines	-0.21	0.12	0.15	-0.32	-0.13	-0.47
	Pine seedlings	-0.14	-0.18	0.37	-0.36	-0.37	-0.42
Ground Cover	Total pines	0.02	-0.52	0.68*	-0.13	0.06	-0.47
	Pine seedlings	-0.24	-0.71*	0.59	-0.1	0.42	-0.24

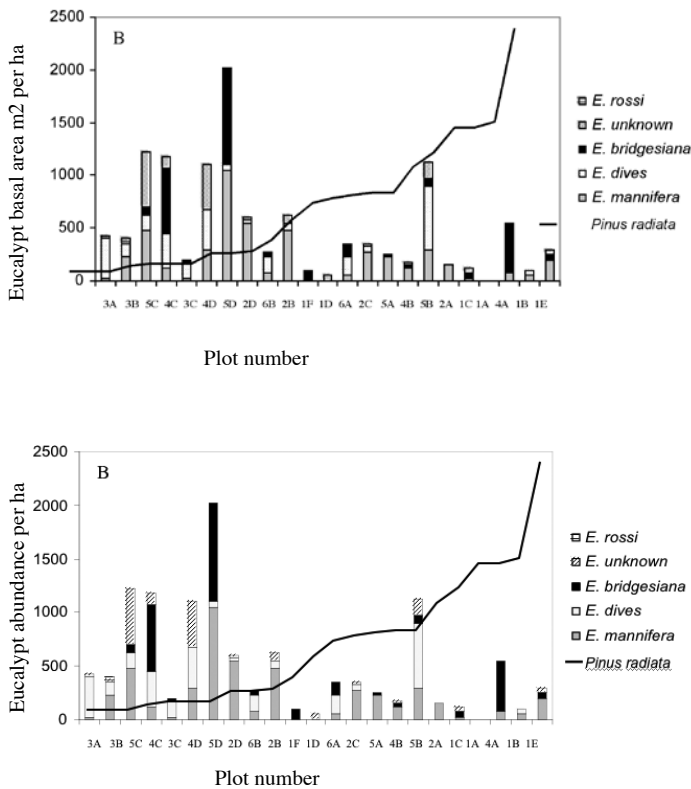


Fig. 9. Eucalypt composition versus increasing pine occurrence at Lidsdale. A. Basal Area m² per hectare and B. Abundance per hectare

The suppression of wildfires in areas surrounding plantations may also be influencing the distribution of pines with respect to the plantation. While mature pines are destroyed by high intensity fires, they are capable of surviving low intensity burns which do not scorch the crown (De Ronde 1982). Prescribed, low intensity fires implemented in areas close to the plantation in order to protect the resource are not of high enough intensity to destroy the pines. At distances away from the plantation high intensity wildfires are capable of killing larger adults. Natural occurrence of fires at a frequency high enough to prevent pines reaching maturity will hinder the success of pines in these areas.

The structure of a forest edge can be critical in determining the invasibility of an area and the removal of understorey vegetation can result in increased seed flux (Cadenasso & Pickett 2001). The process of plantation establishment involving the modification of vegetation in areas surrounding plantations, may be providing the disturbance that is thought to be necessary for the instigation of pine invasions (Richardson et al. 1994b). It is possible that disturbance close to the seed source is facilitating the initial establishment of pines adjacent to the plantation which may then make further spread into undisturbed areas possible. It is also a possibility that these results are confounded by distance. High pine abundances close to the plantation may be attributed to

close proximity to the seed source rather than the effects of disturbance or low levels of species diversity.

The analysis of species composition provided little insight into determinants of pine distribution. Few notable relationships between species assemblages and the level of pine invasion were found. The sole significant result was a separation of pine basal area categories in far plots at Newnes on the basis of total species composition. Plots of medium pine basal area were characterised by a high abundance of *Eucalyptus pauciflora*. This species was only present in one plot suggesting that it is not responsible for wider differences in pine occurrence. Further, the small number of samples included in these categories demands discretion in the interpretation of this result.

The negative relationship between eucalypts and pines witnessed when all plots were pooled suggests the presence of interspecific competition. The greater eucalypt basal area within far plots at Newnes highlights a structural difference of the two vegetation types. If eucalypts and pines are competing for space, it follows that the higher eucalypt presence at Newnes may provide a natural barrier to invasion. This was not the case as mean pine basal area within far plots did not differ significantly between sites (Williams & Wardle 2005).

Contrary to the findings of Lindenmayer and McCarthy (2001), levels of invasion were similar across plots with differing dominant *Eucalyptus* species, indicating that canopy species composition had little influence on pine distribution. The absence of *Eucalyptus piperita* from plots with high pine basal area at Newnes would normally indicate a resistance of this species to invasion. However, plots free of the species were restricted to transect 1, an area characterised by reproductive trees and high seedling numbers. Spatial analysis of these areas revealed evidence for self propagation by wildlings (Williams and Wardle in preparation). This process of regeneration rather than any greater site suitability resulting from the absence of *Eucalyptus piperita* is likely to be responsible for the high pine abundance observed. Similarly, high pine numbers in plots with considerable eucalypt presence were also explained by the occurrence of reproductive trees and high seedling abundance.

Vegetation structure does not appear to be strongly influencing pine distribution. Correlations between percentage cover and pine abundance within all plots at both sites were inconsistent and mostly insignificant suggesting that factors other than vegetation components are driving pine establishment. Division of plots on the basis of distance from the plantation did strengthen some of these relationships returning three significant results, which require further explanation. A significant positive relationship between pine abundance and groundcover was found within far plots at Newnes. Range in groundcover within these plots was high (20–65%) allowing an investigation of its impact on pine presence. While high numbers of pines were associated with higher levels of groundcover, their presence can also be explained by the

occurrence of highly reproductive trees within these plots, yielding large numbers of seedlings.

The significant negative relationship found between pine seedlings and groundcover within adjacent plots at Newnes is consistent with results from other studies. Lindenmayer and McCarthy (2001) found that the incidence of *Pinus radiata* wildlings increased significantly with decreasing groundcover. It is thought that reductions in groundcover diminish competition from neighbouring plants and facilitate pine establishment (Richardson et al. 1994b). A reduction in grass cover, known to compete with pine seedlings (Pearson 1942) can result in higher pine establishment rates. The level of groundcover in an area is often a reflection of other factors which are influencing susceptibility to invasion. It is possible that the negative relationship between seedlings and groundcover reflects high levels of disturbance close to the plantation. However, this relationship was highly influenced by one plot which experienced the lowest level of groundcover (5%) and the highest number of seedlings (86). The plot was located adjacent to the plantation and was highly disturbed, with several large fallen logs and an old trail-bike track. The high level of disturbance here has led to increased light levels and reduced groundcover, creating an environment favourable to seedling establishment.

The significant positive relationship between pine seedlings and canopy cover witnessed in adjacent plots at Lidsdale must be interpreted with caution, as differences in percentage cover between plots were limited and it is improbable that they are capable of causing such large divergences in seedling abundance. An increase in cover from 10% to 15% is unlikely to be the sole factor generating a more than four-fold increase in seedling abundance.

The determining influence of vegetation on pine distribution observed by Rouget et al. (2001) was not witnessed in this study. Relationships between pine occurrence and community characteristics were weak and variable. Many of the patterns reported here can be explained by the presence of reproductive trees that are yielding high numbers of seedlings. Pines were observed growing in plots with vastly different levels of understorey and groundcover implying that these components of the vegetation do not prevent pine seedling establishment. Recent work has found that at local scales, propagule pressure is in fact a better determinant of invasive pine distributions than environmental variables including vegetation type (Rouget & Richardson 2003). Pine plantations provide a large constant seed source capable of exerting enormous propagule pressure on surrounding areas. In addition, highly reproductive wildlings represent an effective secondary seed source. It is possible that the pressure provided by both the plantation source and the first cohort of invaders is high enough to overcome any barriers to establishment created by vegetation (Richardson et al. 1994b) and suggests that wherever plantations are bordered by eucalypt forest, invasion events are likely. Almost one

million hectares of pine plantations are cultivated in Australia placing a significant area of native vegetation under threat. Further study of a greater number of plantation sites will help investigate the relative roles of propagule pressure and vegetation structure and composition on invasion success.

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